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EXPERIMENTAL INTERSEXUALITY AND THE SEX-PROBLEM¹

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UNTIL a comparatively recent time the sex-problem was one of the white spots on the map of biology. There is hardly another problem which has been such a playground of dilettantism, and if we look through the older literature on the sex-problem we find almost as many philosophers and economists inventing sex-theories as there are biologists. But there is scarcely another problem in biology which in the brief period of a decade and a half has emerged from a state of absolute ignorance into one of most hopeful knowledge. The all-important step which has been made during this time is the complete insight into the elementary mechanism which pro-

¹ Evening lecture delivered at the Woods Hole Marine Biological Laboratory, July 28, 1916. The majority of the facts recorded here as well as the principle of their explanation have been published in a series of papers which appeared following a preliminary report in *Sitzungsber. Ges. Morphol. Physiol. München*, 1911, namely: Goldschmidt, R., "Erblichkeitsstudien an Schmetterlingen," I, *Ztschr. induct. Abstammungsl.*, 7, 1912; Goldschmidt, R., u. Poppelbaum, H., "Erblichkeitsstudien an Schmetterlingen," II, *Ibid.*, Vol. 12, 1914; Poppelbaum, H., "Beitraege zur Kenntnis, etc.," *Ibid.*; Goldschmidt, R., "A Preliminary Report, etc.," *Proc. Nat. Ac. Sc.*, I, 1915; Goldschmidt, R., "Genetic Factors and Enzyme Reaction," *Science*, Vol. 43, 1916. See further the related chapters in Goldschmidt, R., "Einführung in die Vererbungswissenschaft," 2. ed., Leipzig, 1913, and in Correns, C., and Goldschmidt, R., "Vererbung und Bestimmung des Geschlechts," Berlin, 1913. A complete account of the entire work, with the necessary illustrations, is in preparation. I am greatly indebted to Dr. R. A. Spaeth for revising this MS.

duces the normal distribution of the two sexes. To-day it is well known to every one how this insight was reached practically simultaneously by the study of Mendelian inheritance and the cytological investigation of the chromosomes and how the two solutions are in most wonderful harmony. The outstanding facts which I regard as one of the corner-stones of modern biology are familiar even to the beginner in biology. Cytologically one of the sexes, the heterogametic sex, contains only one X-chromosome, the other, the homogametic sex, two of them. Every one knows how the maturation division separates entire chromosomes and therefore the heterogametic sex produces two kinds of sex-cells, *i. e.*, with and without X-chromosomes, but the homogametic only one kind, all with X-chromosomes; and how chance-fertilization produces again the two parental combinations, that is, the two sexes. You are furthermore familiar with the fact that the Mendelian experiments yield practically the same result. If we substitute the term "sex-factor" for "X-chromosome" and "hetero-homozygous" for "hetero-homogametic," the facts are identical. One sex is heterozygous for the sex-factors, say Ff; the other homozygous, say FF; the first one produces two kinds of gametes, the second only one, and chance-fertilization results in equal numbers of the parental combinations. The results of experiments on sex-limited inheritance have shown, finally, that both sets of facts are the same thing, only expressed in different language, in other words, that the X-chromosomes are the vehicles for the distribution of the sex-factors. If we state further that there are animals in which the heterozygous sex is the female, and others where it is the male, we know the elementary facts from which any further study of the sex-problem has to start.

Now that we know the elementary mechanism of sex-distribution, can we regard the sex-problem as solved? I do not think so. What are the sex-factors and how do they determine sex? Are the two sexes clean-cut alternatives and is it therefore impossible to transform one

into the other, or are they nothing but limiting points of a series, which might approach each other or even become interchanged? These and many other questions can only be approached by experimental modifications of the normal sex conditions. There is one road towards this goal, the application of the well-known influence of the internal secretion of the sex-glands upon the sex-characters in castration- and transplantation-experiments, as well as the study of analogous experiments by nature. Another approach is rather an unexpected one; this has been followed in my experiments, an account of which I now have the pleasure of giving you.

Insect-breeders have long known that in crosses of species as well as of geographic varieties a comparatively high percentage of sexual abnormalities are produced. Furthermore, any collector of moths knows that similar abnormalities, usually called gynandromorphs or hermaphrodites, appear occasionally in nature and one of the moths in which these occur is the gipsy-moth. Since this moth has a very wide range of geographic distribution through very different climates a considerable difference of geographic varieties is to be expected. Furthermore, as is well known, the sexes are extremely dimorphic. Therefore, seven years ago I began hybridization experiments of European and Japanese gipsies. I was rather fortunate in striking the right forms which gave, from the outset, the most interesting results.

The first result was that crosses of Japanese females with European males yielded normal offspring, whereas in the offspring of the reciprocal cross, European female $\times$ Japanese male, all males were again normal, but all females showed in all parts of their bodies admixtures of male characters. I first called these animals gynandromorphs. But as this term is usually applied to animals with bilateral or antero-posterior or similar mosaic of the two sex-characters, it seems advisable to use another term for these forms, which in general repre-

sent a definite step between the two sexes.² The phenomenon shall therefore be called intersexuality. Further experiments now proved that intersexuality segregates, F_2 giving normal and intersexual animals. It was further shown that in some experiments the females remained normal and the males became intersexual. When the experiments were repeated, however, different results appeared. And as the material used came from different strains, suspicion arose that there are many different races of gipsies, differing in regard to those things which are responsible for the intersexuality. This suspicion was strengthened when it became probable that the peculiar thing responsible for intersexuality could be influenced by external conditions. If this is the case, conditions in Japan ought to be very favorable for an origin of such racial variation, as the Japanese islands show climatic conditions varying from an almost arctic to an almost tropical climate. These suppositions turned out to be correct, as was proved by the further study of these questions in Japan in 1914 and with the material brought from there to this country.

In order to make the results clearer and their bearing on the sex-problem more evident, I want to apply just the opposite method from that used in the research work, and to give first the general interpretation of the results, which differs only in a few points from that used since 1911, and then the experimental facts from which it has been derived. What we have to explain is that two nearly related forms, both normal in regard to sex-inheritance, produce, if crossed in one direction, normal offspring, in the other direction, normal males and intersexual females; (2) that, as we may now say, the degree of intersexuality is definite in a given cross, but different in different crosses; (3) that intersexuality shows Mendelian segregation; (4) that males may become intersexual too in certain crosses.

The explanation for these and the other facts later to

² The special meaning of this will be discussed in another paper in connection with very interesting new facts.

be reported is the following: Both sexes contain the anlagen for either sex. In both sexes, irrespective of the zygotic constitution, both anlagen might become patent. Which one is to appear depends entirely upon the quantitative relation of both.³ If we apply the usual symbols and keep in mind that the female sex is here the heterozygous one we have the following formulæ:

$$\boxed{\text{FF}} \text{ Mm} = \text{♀}, \quad \boxed{\text{FF}} \text{ MM} = \text{♂}.$$

(It will soon be explained why the female set FF is put in a square.) The female set as well as the male set act independently and with a definite quantitative strength. In order to have a convenient term we call this quantitative value of the sex-factors their potency or valency.

³ The idea that sex-determination is a quantitative rather than a qualitative process is of course not new. Practically all writers about the cytology of sex-determination have developed such ideas, beside the well-known old and new metabolistic theories. Such a quantitative view was proposed by myself in 1904 ("Der Chromidialapparat, etc.," *Zool. Jahrb. (An.)*, 21) and more fully developed in 1910 ("Kleine Beobachtungen, etc.," *Arch. Zellf.*, 6). Other such theories were proposed by R. Hertwig, 1905-07 ("Ueber das Problem der Sexuellen Differenzierung, etc.," *Verhdlg. deutsche Zool. Ges.*, 1905, 1906, 1907), based on his views about the nuclear-plasmic relation. Again others of a strictly quantitative character were discussed by E. B. Wilson ("Studies on Chromosomes," III, *Journal Exp. Zool.*, 3, 1906), by Th. Montgomery, Jr. ("Chromosomes in the Spermatogenesis, etc.," *Trans. Amer. Phil. Soc.*, 21, 1906), and by Th. Boveri ("Ueber Beziehungen des Chromatins zur Geschlechtsbestimmung Sitzber. physikal. medicin. Ges. Würzburg," 1908-09). A full discussion of the relative values of qualitative and quantitative views in regard to sex-determination is given by Th. H. Morgan ("A Biological and Cytological Study, etc.," *Jour. Exp. Zool.*, 7, 1909), who decides for the latter. However, I think that all these authors no longer cling to the details of their former views. The first attempt to prove a quantitative theory of sex-determination experimentally has been made by R. Hertwig in his well-known experiments with frogs (since 1905). Quite another type of theory, practically the same as is to be used in this paper, combining the quantitative view with the Mendelian and cytological results, has been developed on an experimental basis in my papers from 1911 and 1912 (*l. c.*) and has been adopted by many writers (*i. e.*, Doncaster and Harrison, Standfuss, Witschi). A third view has since been developed by Riddle in a series of preliminary papers (Carnegie Year Book, 1913, *Science*, Vol. 39, 1914, *AMER. NATUR.*, Vol. 50, 1916, etc.). His theory is based partly on chemical studies of pigeon eggs, partly on hybridization experiments with doves. It is not impossible that in the latter something like intersexuality is produced, if I understand the short accounts thus far published.

If you like to form a definite idea you might assume that the potency means a certain concentration of enzyme which acts according to well-known laws.⁴ In order to make the situation clear we assume that we are able to measure their potency. And we find that the female factorial set $\boxed{\text{FF}}$ is 80 units strong and every male factor $\text{M} = 60$ units. Then in the female formula $\boxed{\text{FF}}$ Mm the female set overpowers the one M present by 20 units, whereas in the male formula $\boxed{\text{FF}}$ MM the two Ms with the value of 120 are 40 units stronger than $\boxed{\text{FF}} = 80$. Now we face two possibilities. Either the slightest preponderance of one set over the other, say by only one unit, is sufficient to determine the male or female sex, or there is a definite minimum of preponderance necessary—we call it the epistatic minimum—beyond which one or the other sex appears. Let us now suppose this minimum to be 20 units. Then of course 40 units are left between the two extremes male-female preponderance. If we call the difference value between the male and female factorial set e , then we have a female, when $\boxed{\text{FF}} - \text{M} = > 20$ and a male, when $\text{MM} - \boxed{\text{FF}} > 20$, or in other words the limiting values for e for the two sexes are $+20$ and -20 . We can now express this conception graphically in the following diagram, where the values

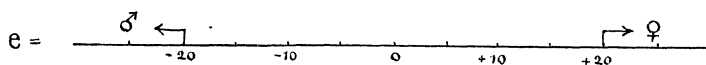


FIG. 1

of e are arranged on a straight line. Individuals to the right of $+20$ are females, to the left of -20 are males. But what of the intermediate points? These are the intersexual animals; if they are heterozygous for M they are intersexual females and if they are homozygous for M they are intersexual males. How does this diagram now

⁴For proof that this conception comes near the truth see Goldschmidt, R., "Genetic Factors and Enzyme Reaction," *Science*, N. S., 43, No. 1099, 1916. Very important new facts will be published later, which will probably enable us to replace the symbolistic Mendelian language, used here, by more definite physico-chemical conceptions.

explain the fundamental experiment? Suppose we have two races both normal in regard to the quantitative behavior of their sex-factors, but with different absolute values of the potencies. The values are supposed to be the following:

Weak European Race			Strong Japanese Race		
♀	$\boxed{FF}$	Mm	$\boxed{FF}$	Mm	
	80	60	100	80	
♂	$\boxed{FF}$	MM	$\boxed{FF}$	MM	
	80	60 60	100	80 80	

It is evident that both races, if bred true, behave normally. Here we must now add that the female factors or anlagen are inherited exclusively maternally, without any paternal influence. Therefore the square. But the M's are typical Mendelian sex-factors. Let us cross now a Japanese ♀ with an European ♂. F_1 is then

$$F_1 \text{ ♀ } \boxed{FF} \text{ Mm, } F_1 \text{ ♂ } \boxed{FF} \text{ MM.}$$

100 60 100 80 60

The value e is then $+$ and -40 , the offspring is normal. The reciprocal cross European female with Japanese male gives

$$F_1 \text{ ♀ } \boxed{FF} \text{ Mm, } F_1 \text{ ♂ } \boxed{FF} \text{ MM.}$$

80 80 80 80 60

Now we see that in the female e or $FF-M=0$. The animal is intersexual, exactly half-way between male and female.

Instead of deriving further theoretical expectations we shall now see how the experimental facts fit these general conceptions of a quantitative nature of sex-determination. The first point is of course the question of the different absolute and relative potencies. There are primarily two ways open for testing it. One is to influence these potencies experimentally. Only a few preliminary steps in this direction have thus far been made,

which may be omitted here. Another way would be to find many races which differ constantly in regard to the potency of these factors, which could be shown by the results of cross-breeding. The expectations are, then, that with increasing value of M , in crosses, where these races are used as males in combination with "weak" females, a corresponding type of female intersexuality must appear, giving a complete series from femaleness to maleness. And if we can find a race with so high a potency of M , that the combination lies beyond the epistatic minimum for maleness, then all the would-be females will be transformed into males. I now have at hand such races from Europe and Japan and can produce at will and in 100 per cent. of the offspring all grades between the two sexes. Thus we have one Japanese race, the race G , medium strong in regard to the potency of the factor M . If we cross these males with females of the Japanese race K , which shows comparatively low potency of the female factorial set, all would-be females in F_1 are slightly intersexual. We might put them at the point $+15$ in our diagram (Fig. 1). Their antennæ are feathered, but less than in males, a portion of the wings assumes the brown color of the male, there are not as many eggs as in a normal female, but the mating instincts as well as the copulatory organs are still female and the eggs may be normally fertilized. Then there is a European race F and a Japanese race H , both with a still lower potency of the female factorial set. If we cross these with the same Japanese males G we get somewhat slighter female intersexuality. All secondary sex-characters are more male-like; the instincts are still female and the animals attract the males and mate. Then one of the characteristic hairy egg sponges is laid, but it contains no eggs, only hairs. The copulatory organs are already changed in the direction of the male and no successful mating and egg deposition is possible, although the abdomen is filled with ripe eggs. Then there is another European race F with very low potency of the female factors. If we mate these with the same males G ,

intersexual females appear which are more than half-way between males and females. The secondary sex-characters are almost male. The instincts and behavior are about intermediate between the sexes. Males are scarcely attracted or not at all and no mating occurs. The copulatory organs show the strangest combinations of the male and female types, but there are still typical but rudimentary ovaries left. There is now another Japanese race in my possession, the race X. This one exhibits a still higher potency of the male factor M. If we cross this one with the European race F, a still higher degree of intersexuality appears. Now we have animals which externally are almost indistinguishable from true males. But certain characters, especially in the copulatory organs, still show their female origin. The instincts are entirely male and they try—always unsuccessfully—to mate with females. But the most interesting feature is the sex gland. This is a body looking externally like a testis, but showing in sections every single step between an ovary with nothing but immature eggs through a mixture of ovarian and testis tissue to a real testis. This is of course the highest grade of intersexuality which can be reached. The next step would be the complete transformation of the would-be females into males. And this can be obtained too. I have two Japanese races O and A which show such a high potency of M that crossed with any European females and the Japanese females H they produce nothing but males, all would-be females being converted into males.⁵

⁵ It might be added here that two different lines of female intersexuality can be distinguished in regard to the most conspicuous feature, the color of the wings. In one line intersexuality begins with white wings, then dark cunei appear on the wings; they grow larger and larger, forming streaks along the veins until finally only fine white spots are left on a dark wing. The second series shows even in the first grades of intersexuality male color all over the wings without any streak formation. Which type appears depends on both races involved, and is due to physiological conditions in regard to pigment formation which are not yet entirely clear. The intersexual males always exhibit the first type. Color photographs of an almost complete series of the second type are given in my papers from 1912 and 1914. Photographs of the first type in the female series are not yet published. A complete series of the transformation of the female copulatory

I think these facts alone would be sufficient to prove that the above given quantitative conception of sex-determination is the right one. But we can quote furthermore a real experimentum crucis. We have seen that the very weak European race F crossed with the medium strong Japanese males G give a fairly high grade of intersexual females. In our diagram of the values of e we might put them at the point -10 (Fig. 2). The same

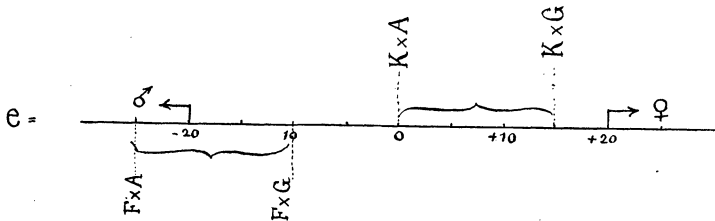


FIG. 2

weak females crossed with the very strongest males A gave nothing but males, the would-be females standing now on the point, say -25 . Now the strongest of the weak races in regard to FF, i. e., the Japanese race K, gave with these same males G slight female intersexualism, say at point $+15$. If our conception is right, the same females, crossed with the very strong males A, ought to give medium intersexual females, to be put at the point 0. And this is the actual result.⁶

Now we have reached a point where we want to know how the complexes $\boxed{\text{FF}}$ and M are inherited. Anybody familiar with Mendelian analysis knows which results are to be expected if F and M are independent Mendelian factors. These tests, so far as fertility allows them to be

organs based on our material is pictured in the paper of Poppelbaum (*l. c.*). Photomicrographs of the transition from an ovary to a testis are given in my paper of 1914. In regard to the occasional appearance of a single normal female in cultures where all females are transformed into males, see our publication in the *Proc. Nat. Ac.* It was supposed that they originated from a case of "non-disjunction." Their behavior in breeding does not agree with this supposition but suggests another explanation, which at the same time explains the occasional appearance of intersexual males in nature. Details can not be given without a lengthy discussion.

⁶It might be added that a similar experiment can be performed with the Massachusetts race, which behaves about like the Japanese race K.

made, prove, of course according to expectation, that the factor M is Mendelian and carried in the X chromosome. All results of F_2 and back crosses agree in this point. But what is $\boxed{FF}$? Originally I believed that I could prove its Mendelian character too. This was a mistake, produced by the interference of another phenomenon, connected with the wing-color inheritance. The experiments made since my first communications prove thus far that the complex $\boxed{FF}$ is inherited only through the mother, maternal grandmother, etc., *i. e.*, in the protoplasm of the egg.

We are now prepared to consider the production of the intersexual males, thus far omitted in our discussion. A series of them has been produced extending almost to femaleness. They are easily distinguishable from intersexual females (a point which is of special interest; one explanation being that factors contained in the Y chromosome are responsible for it). The intersexual males always exhibit the first of the above-mentioned (foot-note page 713) types in regard to wing coloration, white streaks appearing on the dark wings. While the wings assume more and more the female shape, the dark color becomes confined gradually to the wing venation, and in the extreme types thus far bred only a few brown spots appear upon some veins. All the other characters, like size of abdomen and copulatory organs, change hand in hand with this. But the behavior of the sex glands is not yet clear. In low grades of male intersexuality the testis always contains some ovarian tissue.⁷ But the highest grade intersexual males of almost female exterior contained a paired⁸ sex gland of somewhat testis character, filled with giant bundles of apyrene spermatozoa, and containing no eggs.

If we now deduce from our general interpretation how these interesting males might be produced, we realize that

⁷ See picture in Poppelbaum's paper. The lower grades of male intersexuality are photographed in our papers from 1912 and 1914. Pictures of the higher grades are not yet published.

⁸ The ripe testis is an unpaired organ.

they are expected to appear when $\boxed{FF}$ is comparatively high in potency and MM comparatively low. There are two possibilities for this event. (1) If we revert to our original example of a cross between weak European and strong Japanese races, we have in one direction:

$$\begin{array}{ccc} \text{Eu. } \text{♀} & \times & \text{Jap. } \text{♂} \\ \boxed{FF} \text{ Mm} & \times & \boxed{FF} \text{ MM.} \\ 80 \quad 60 & & 100 \quad 80 \quad 80 \end{array}$$

As $\boxed{FF}$ is inherited maternally, any generation of this cross will have the weak set $\boxed{FF} = 80$. There is no combination of two M's possible which is not at least 20 units higher than FF, therefore no intersexual males can occur. Now take the reciprocal cross:

$$\begin{array}{ccc} \text{Jap. } \text{♀} & \times & \text{Eu. } \text{♂} \\ \boxed{FF} \text{ Mm} & \times & \boxed{FF} \text{ MM.} \\ 100 \quad 80 & & 80 \quad 60 \quad 60 \end{array}$$

The F_1 males are $\boxed{FF}$ MM and therefore normal, as
100 80 60

$e = -40$. F_2 from this cross has again the maternal and grandmaternal set $\boxed{FF} = 100$. The Mendelian factors MM are recombined and we get the combinations:

$$\begin{array}{ccc} \text{MM} & \text{and} & \text{MM.} \\ 80 \quad 60 & & 60 \quad 60 \end{array}$$

The latter males are therefore:

$$\begin{array}{ccc} \boxed{FF} & & \text{MM.} \\ 100 & 60 & 60 \end{array}$$

This means that e has just the limiting value -20 . It follows, that if we have two races, in which the relative values differ only slightly from this example to the disadvantage of the weaker M, say $M = 59$ instead of 60, male intersexuality is to be expected in the F_2 generation of a cross, where the mother belongs to the stronger race. This is indeed one of the actual facts.

According to the above derived formulæ these intersexual males ought to number exactly one half of the

male individuals. But this has so far never been the case. In order to understand it we have to point now to a fact which we omitted in our previous discussions. We have located the intersexual animals, males and females, at a certain point between the two sexes, as represented in the two diagrams. But in fact these points are only the mean of a certain range of variation in regard to the grade of their intersexuality. Whether this means that the potencies of the factors are variable or only their ultimate effect shows variation produced through influences during the development, is a question not to be discussed here. The fact is, however it might be caused, that the value of e as the measure of intersexuality, is variable around a mean. If this is the case, the following expectations are to occur (Fig. 3): If the values of e

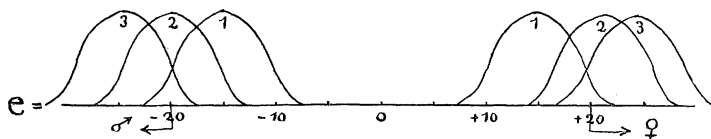


FIG. 3

approach the epistatic minimum (20 and -20 in our diagram), then a point must be reached where the variability-curve stretches beyond this limit. That means—curve 1—that in cases of low grade intersexuality some $+$ or $-$ individuals might overlap into the normal. Of course any position of these curves and a corresponding numerical relation of normals and very slightly intersexual animals might be met with, as the curves 2 and 3, Fig. 3, indicate. And indeed such cases have been found as well on the female as on the male side. Types of this kind, realized in the F_2 crosses with male intersexuality, are those with which we have dealt in the previous paragraph. Thus far all facts agree with this conception, in one culture up to F_5 . Further checks are in progress.

But there is another possibility for the production of intersexual males. Let us assume that we could find two races of the following constitution:

$$\begin{array}{lcl} \text{Strong race } \text{♀} = \boxed{\text{FF}} \text{ Mm} & \text{♂} = \boxed{\text{FF}} & \text{MM} \\ & 100 \quad 60 & 100 \quad 60 \quad 60 \end{array}$$

$$\begin{array}{ccc} \text{Weak race} & \text{♀} = \boxed{\text{FF}} & \text{Mm} & \text{♂} = \boxed{\text{FF}} & \text{MM.} \\ & 80 & 50 & 80 & 50 \quad 50 \end{array}$$

The F_1 cross of these, using the strong race as mother, would give:

$$\begin{array}{ccc} F_1 \text{ ♀} & \boxed{\text{FF}} & \text{Mm} = \text{normal female,} \\ & 100 & 50 \end{array}$$

$$\begin{array}{ccc} F_1 \text{ ♂} & \boxed{\text{FF}} & \text{MM} = \text{intersexual male, as } e = -10. \\ & 100 & 60 \quad 50 \end{array}$$

Every single male ought to be intersexual. Through the kindness of Dr. Machida in Tokyo, who first has reached this strange result, I could bring back from Japan two such races and they breed exactly according to expectation.

This is about the skeleton of our work around which of course many interesting experimental, morphological, embryological, cytological and physiological facts are grouped. I am rather optimistic in regard to the general conclusions, which might be drawn from these facts as well as regards the sex-problem as on some fundamental questions of heredity. Combining these facts with the work on hormone action as related to sex we can, I think, form a pretty clear idea about sex-differentiation and determination.⁹

If we put them in line with the facts of experimental embryology concerning the determination problem we see the outlines of a promising theory of heredity. But this can be discussed only when a full account of the work has been given.

⁹ The relation of gametic or zygotic intersexuality to the hormonal intersexuality produced in castration and transplantation-experiments in Crustacea, birds and mammals (especially the work of G. Smith and Steinach) to which now, after F. Lillie's discoveries, the case of the free-martin has to be added, has been worked out in the chapter on Sex in my treatise on genetics (*l. c.*), 2d edition. A detailed comparison between the moth-work and the facts known about human intersexuality, containing, too, a discussion of the relations of zygotic and hormonal intersexuality, was sent to Germany for publication about half a year ago, but it is not known whether it has been published there or adorns the waste-paper basket of His Britannic Majesty's censor.